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THE COMPARATIVE ANATOMY OF THE SNOUT IN RHIPIDISTIAN FISHES

By KEITH STEWART THOMSON

No. 10 — *The comparative anatomy of the snout in rhipidistian fishes*

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INTRODUCTION

Due mainly to the work of Goodrich and Gregory it is now almost universally accepted that the Rhipidistia (fossil fishes of the order Crossopterygii, in the system of Romer, 1955) are the closest ancestors of the tetrapods. In general it has been assumed that the first tetrapods, the Amphibia, were of mono- phyletic origin, but certain theories of a diphyletic origin have been proposed. It has been argued that, of the living Amphibia, the Urodela and Anura represent two distinct lineages. Also, while the fossil history of the Recent Amphibia is very incom- plete, it has been noted that the two major groups of Palaeozoic amphibians, the Apsidospondyli and the Lepospondyli, have yet to be shown to have a common ancestor. Both Säve-Söderbergh and Holmgren proposed a diphyletic theory whereby the Dipnoi were stated to be the ancestors of the Urodela and the Rhipidistia the ancestors of the Anura. This theory is not now generally accepted. A second diphyletic theory is that of Jarvik (1942) who, while rejecting the Dipnoi as possible ancestors, proposed that the Urodela and Anura arose from separate stocks of Rhi- pidistia. It is with this theory that the present investigation is concerned.

From a study of the snout anatomy of the Rhipidistia and a review of the anatomy of the snout in other gnathostomes, Jarvik (1942) concluded that the Rhipidistia comprise two separate stocks—the "Porolepiformes" (families Porolepidae and Holop- tychidae) and the "Osteolepiformes" (family Osteolepidae and Rhizodontidae). Jarvik studied the Lower Devonian genus *Porolepis* as his type of the "Porolepiformes" and the Upper Devonian rhizodontid genus *Eusthenopteron* as his type of the "Osteolepiformes." He gives a detailed account of the snout anatomy of these two forms and of the differences between them. He considers that the differences he observed indicate a basic split in the Rhipidistia. Further studies (1962) have elaborated this theory.

Jarvik claims that the two groups of Rhipidistia gave rise

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independently to tetrapod vertebrates — the ''Porolepiformes'' to the Urodela, and the ''Osteolepiformes'' to the Anura and probably to all other vertebrates. Jarvik's evidence for this is that from an extensive review of the snout anatomy in certain Amphibia he concluded not only that the Urodela were fundamentally different from the Anura, but that the diagnostic features of distinction between the two ''types'' of snout anatomy could be identified in the two ''stocks'' of Rhipidistia also. Thus he believes that the supposedly ''characteristic'' natures of the snouts of ''porolepiform'' and ''osteolepiform'' rhipidistians have survived essentially unchanged in the Recent amphibians.

In general there has been hesitation in accepting Jarvik's conclusions because, in the first place, it is only the snout region that has been studied in detail and examination of the entire anatomy might yield different results, and, in the second place, because the comparisons made were rather limited in scope. Of the Amphibia only *Salamandra* and *Rana* were discussed in detail, and, even more important, of the Rhipidistia only *Porolepis* and *Eusthenopteron* were available for study.

The present paper is concerned primarily with the evidence for a basic distinction between the ''Porolepiformes'' and the ''Osteolepiformes,'' for all subsequent phylogenetic hypothesis must rest upon the validity of this proposed dichotomy.

For many Rhipidistia there is little material preserved in a fashion suitable for detailed palaeo-anatomical studies, but of the osteolepid genus *Ectosteorhachis* (previously confused with *Megalichthys*, see Thomson, 1964) from the Lower Permian of North America, much well preserved material exists. I have used this material to prepare a detailed account of the snout anatomy of *Ectosteorhachis*. The knowledge gained from this study, together with other information concerning different genera of Rhipidistia (Ørvig, 1957; Vorobjeva, 1959, 1960a, 1960b; Kulczycki, 1960; Thomson, 1962; Jarvik, 1962) which has become available since the date of Jarvik's original work, enables us to view the anatomy of the Rhipidistia from a broad and more truly comparative basis. The last section of this paper is a critical re-evaluation of Jarvik's theory in the light of this comparative study. Since the basis for Jarvik's theory was evidence from the nasal/ethmoid anatomy of the Rhipidistia, the present investigation is naturally centered in this region.

This study forms part of the work presented to the Department of Biology at Harvard University in fulfillment of the

MATERIALS AND METHODS

The material of *Ectosteorhachis* used in this study comes from the collection of the Museum of Comparative Zoology at Harvard University. It has been collected in the Lower Permian "red-beds" of North Central Texas; several specimens of this collection were used in a previous study of *Ectosteorhachis* ("*Megalichthys*") made by Romer (1937).

The major part of the study has been made from a particularly complete skull (MCZ 8662) from the Belle Plains Formation, Wichita Group, Archer County, Texas, that was sectioned transversely at one-quarter millimetre intervals by the celloidin peel method. Experiments were made to stain the sections: a saturated solution of Alizarin Red S in 95 per cent ethyl alcohol used after the section had been oxidised by immersion in 0.25 per cent potassium permanganate gave the best results, but in general it was found that direct examination of the unstained section under a microscope was the best method of studying the sections. Wax-plate reconstructions were made of the snout region.

I have also used the series of sections made in the horizontal and sagittal planes previously prepared by Dr. Romer (cf. Romer, 1937).

Of other Osteolepidae, and of the Rhizodontidae, Porolepidae and the Holoptychidae, I have studied the collections of the Museum of Comparative Zoology at Harvard University, the American Museum of Natural History, the Chicago Natural History Museum, the British Museum (Natural History) and the Royal Swedish Natural History Museum.

ECTOSTEORHACHIS
Skeleton of the Snout Region

Dermal bones of the skull roof and palate. A full description of the dermal bones of the ethmoid region of the skull of *Ectosteorhachis* has already been given (Thomson, 1964). As shown in Figure 3, the dermal skull roof consists, in the ethmoid region, of a pair of parietal bones which bear the supraorbital lateral line canals forwards and mesially from the dermosphenotics; a single median postrostral bone; paired anterior postrostral bones; a compound naso-rostro-premaxilla (termed "premaxilla" throughout this paper); a lachrymal bone; prenarial and postnarial bones; and a series of four separate nasal bones which bear the supraorbital lateral lines, on each side, from the parietals forward to the ethmoid commissure with the infraorbital lateral line. The infraorbital lateral line canal, on each side, runs in a shallow loop, ventral to the naris and the pre- and postnarial bones, in its passage between the lachrymal and the premaxilla.

On the palate the vomers are roughly triangular in shape (Fig. 4) and the tooth-bearing ridge of the parasphenoid ends anteriorly at the level of the postnasal wall. The vomers form the posterior margin of an "anterior palatal recess" — a shallow recess formed between the anterior margin of the ethmoid endocranium and the premaxillae. The expanded bases of a pair of premaxillary "tusks," in the midline, separate the recess into two parts. The functional significance of the anterior palatal recesses will be discussed later.

External features of the endocranium. The endocranium of *Ectosteorhachis* has already been described in some detail by Romer (1937, pp. 18-22). My purpose here is therefore to add to Romer's account those details of structure not shown in his material, which was incomplete in the nasal region.

Figures 1 and 2 show the overall configuration of the endocranium. The nasal capsules of *Ectosteorhachis* are complete dorsally and laterally except for the foramina for the exit of various canals for nerves from the nasal cavity (e.g. **Fig. 1,** *f.ap.*). The anterior wall and the posterior wall of the capsule are pierced by canals for various nerves and vessels (discussed in the next section); the lateral wall is broken only by the fenestra endonarina. The median wall of the capsule is formed by the solid internasal wall; this is pierced by the canals carrying the olfactory tract and also by several vascular and nervous pathways.

The roof and very thin side walls of the nasal capsule are, for the most part, fused with the overlying dermal bones. On the medial face of the lateral wall of the capsule, immediately posterior to the fenestra endonarina, there is a small elliptically-shaped ridge of endocranial bone projecting into the nasal cavity. This ridge, which I have termed the crista lateralis (Figs. 5, 9, *c.l.*), bears on its median face a groove (Figs. 5, 9, *gr.c.l.*) which, from its relation to the external narial aperture, may have partially enclosed the tube for the external naris.

The posterior wall of the capsule, in addition to being pierced by the canals which in all probability carried the ophthalmicus superficialis seventh and profundus fifth nerves mentioned by Romer (1937), has a large opening in the ventrolateral corner (Figs. 3, 4, 5, 10 D and E, *p.v.f.*) — the posteroventral fenestra — the significance of which is rather enigmatical. Jarvik considered a similar fenestra in *Eusthenopteron* to represent a
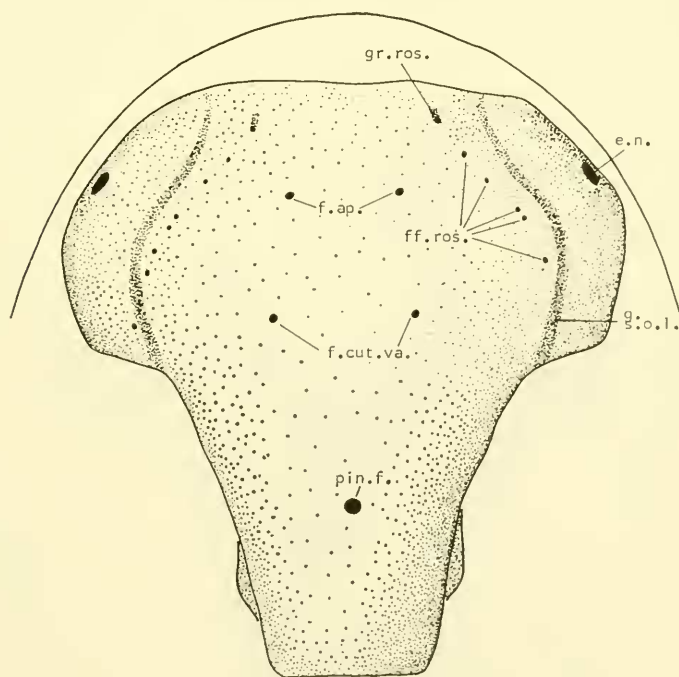

Figure 1. *Ectosteorhachis.* Ethmoid endocranium in dorsal view.

modified posterior external naris which might possibly be connected by means of a duct (the forerunner of the tetrapod naso-lachrymal duct) with the orbital opening. It is not impossible that this fenestra served to permit the passage to and from the nasal cavity of large blood vessels.

The ventral wall of the nasal capsule is not preserved in any of the material studied by Dr. Romer or myself. In view of the otherwise excellent preservation of the specimens it seems most likely that the solum nasi was not ossified but was present in the living animal only in a cartilaginous form. The position of the choana may easily be inferred from the relative positions of the vomer, palato-quadrate and the dermal bones of the cheek.

The pars autopalatina of the palato-quadrate was inserted into the notch formed between the median part of the postnasal wall and the endocranium (Fig. 2, *n. pq.*). This notch is not lined with periosteal bone like the rest of the nasal region and it is possible that the junction between the endocranium and the palato-quadrate in this region was not a free articulation.
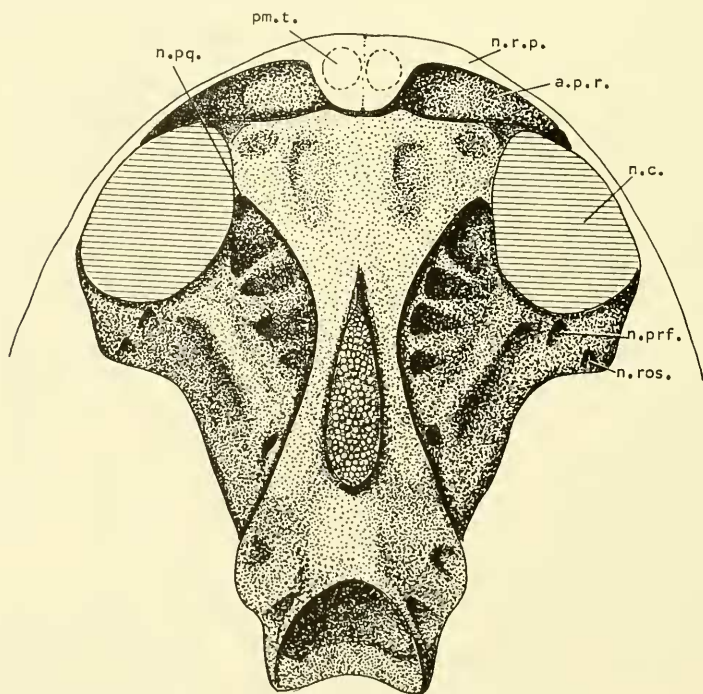

Figure 2. *Ectosteorhachis.* Ethmoid endocranium in ventral view.

The endocranial and associated cavities. In Figures 3 and 4, which show the general configuration of the endocranial cavities, the details of the hypophysial region have been restored, without modification, after the account of Romer (1937, figs. 9, 10).

The cranial cavity in the ethmoid division of the skull of *Ectosteorhachis* consists of spaces containing the hypophysial and pineal regions and the olfactory tracts. Since there is no part of the forebrain corresponding to the olfactory bulbs, it is assumed that the olfactory bulbs are represented by swellings in the canals for the olfactory tracts, as is the case in the Dipnoi (cf. Pinkus, 1895). There is no continuation of the cranial cavity anterior to the point of separation of the two olfactory tracts; the internasal wall contains no large cavities.

Immediately anterior to the level of the separation of the olfactory tracts there arises, from the ventral surface of the canal for each tract, a set of fine canals (Fig. 4, *cc.mea.*, *c.ana.*) that I have interpreted, judging from their position and distribution, as having carried vessels probably connected with the internal carotid artery. There are two sets of canals. A series of smaller ramifying canals pass forwards medial and ventral to the olfactory tract canal and terminate in the highly cancellous internasal wall (Fig. 4, *cc. mea.*). A single larger canal immediately separates from the smaller canals and runs forwards (Fig. 4, *c.ana.*) ventral to the olfactory tract canal; at a point just posterior to the nasal cavity it recombines with this canal.

Another set of canals arises from the dorsal surface of the canal for the olfactory tract just posterior to the nasal capsule; these canals (Fig. 3, *c.m.cut.va.*, *c.l.cut.va.*) seem also to have contained vascular elements and extend in three directions in the endocranium. (1) An anterior canal has a short connection back to the canal for the olfactory tract and a stout branch curving forwards over the nasal sac. It has a short cross-connection to the canal for the ophthalmicus superficialis seventh nerve (see below), as it passes through and above the postnasal wall. According to Romer (1937) there is a complete fusion of the two canals here and they enter the nasal cavity together. My material indicates, however, that the canals are distinct from each other and from the nasal cavity. The anterior canal disappears in the anterior part of the endocranium medial to the nasal capsule. (2) A median canal (Fig. 3, *c.m.cut.va.*) passes anteromedially and opens onto the dorsal surface of the endocranium below the median postrostral bone of the dermal skull

roof (Fig. 3, *m.pr.*). (3) A lateral canal terminates in the lateral part of the endocranium behind the nasal cavity (Fig. 3, *c.l.cut.va.*).

Romer (1937, p. 32) has already noted that the posterior wall of the nasal capsule is pierced by two canals which seem to have carried the ophthalmicus superficialis VII and profundus

Figure 3. *Ectosteorhachis.* Endocranial cavities and the dermal bones of the skull roof. Dorsal view.

V cranial nerves, the canal for the former lying dorsolateral of the canal for the latter. The canal for the profundus V (Fig. 3, *c.pr.V*) is a short simple tube through the postnasal wall; there is a slight connection within the postnasal wall with the canal for the ophthalmicus superficialis VII. The latter canal is entirely separate from the nasal cavity, within the postnasal wall. In addition to the connection with the canal for the profundus V and the anterior vascular canal noted above, there is given off from the canal for the ophthalmicus superficialis VII the first of

a series of dorsal branches which pass out of the endocranium
(Fig. 1, *ff.ros.*) and obviously contained branches of the nerve
supplying the sense organs of the supraorbital lateral line canal.
The canal for the ophthalmicus superficialis VII curves forwards
through the roof of the nasal capsule and emerges from the
endocranium at about the level of the anterior nasal wall and
thence continues in the space between the endocranium and the
dermal bones.

The anterior wall of the nasal capsule is pierced by a series
of fine canals (Figs. 3, 4, *cc.aa.*) which communicate with the
palatal recess and the medial surface of the premaxilla.

A fine canal (Fig. 3, *c.lat.*) passes through the posterolateral
corner of the nasal capsule from the medial surface of the
lachrymal bone without entering the nasal cavity.

The medial wall of the capsule is pierced by two nerve canals
in addition to the canal for the olfactory tract. The more pos-
terior of the two canals (Fig. 3, *c.r.ext.*) leaves the nasal cavity
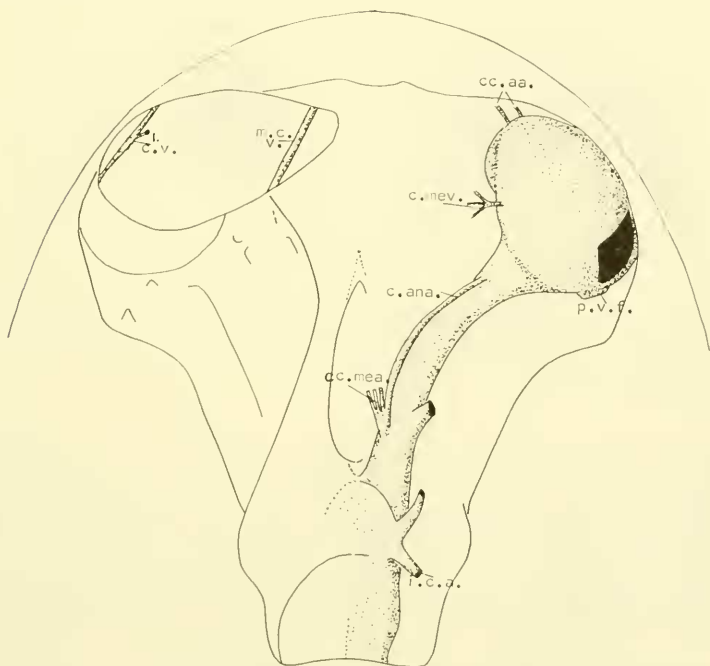

Figure 4. *Ectosteorhachis.* Endocranial cavities and dermal bones of
palate. Ventral view.

just anterior to the canal for the olfactory tract and passes
dorsally, anteriorly and medially to open at the foramen apicale
on the dorsal surface of the endocranium (Fig. 1, *f.ap.*). Romer
considered that the foramen apicale was the opening of the canal
for the ophthalmicus superficialis VII, but the situation of this
canal seems to indicate that it contained the ramus exterior of
the profundus V nerve (discussion below). The more anterior
canal piercing the medial nasal wall leaves the nasal cavity at
the dorsal part of the anteromedial recess (discussed below).
This canal (Fig. 3, *c.r.r.*) passes anteriorly to emerge on the
anterior margin of the endocranium dorsal to the anterior
palatal recess; it seems to have carried an anterior branch of the
profundus V system.

Also opening through the medial wall of the capsule is a set
of branching canals (Fig. 4, *c.mev.*) which ramify within the
internasal septum. This canal system probably contained a set
of veins draining into the nasal cavity.

Figure 5. *Ectosteorhachis.* Nasal cavity. A. Left cavity in anterior view.
B. Left cavity in posterior view. Graphical reconstructions from the
sectioned specimen.

The nasal cavity itself is roughly elliptical in shape with
the long axis of the ellipse lying at an angle of about 45° to the
anteroposterior axis of the head. The inner surface of the nasal
capsule is not ornamented and the only modifications of the
otherwise smooth contour of its surface are caused by the pos-
terior median recess (Fig. 5, *p.rec.*) into which the olfactory
tract entered, and an anterior median recess (Fig. 5, *a.m.r.*)
(termed the ventromedial recess by Romer, and already discussed
by that author). The crista lateralis broadly separates a choanal

recess from the rest of the nasal chamber. The groove on the median surface of the crista lateralis may have borne a short narial tube connecting the naris and the nasal chamber (Fig. 3, *n.t.*).

Certain of the dermal bones contain cavities which are clearly related to the canals for nerves and vessels which pass through the endocranium.

Each vomer is pierced by a medial and a lateral canal (Fig. 4, *m.c.v.*, *l.c.v.*) which are occasionally branched. There are no cross-connections between the canals, but the lateral canal, on one side of the specimen sectioned, has a dorsal branch which emerges on the dorsal face of the vomer underneath the nasal cavity. Since the solum nasi is not preserved it is not possible to detect whether or not this branch actually connected with the nasal cavity.

Neither vomerine canal can be traced posteriorly; it is assumed that the medial canal would have been continued medial to the palato-quadrate complex, between it and the parasphenoid bone, and it probably contained the palatine ramus of the seventh cranial nerve. The lateral canal must have been continued backwards lateral to the choana and between the palato-quadrate and the lachrymal; this canal probably contained the maxillary ramus of the fifth cranial nerve.

The nasal, parietal, premaxillary and lachrymal bones of the skull roof enclose a large canal (Fig. 8, *c.l.l.*) which, from its pathway over the skull roof, its relation to the course of the canal for the ophthalmicus superficialis VII nerve, and the disposition of its fine branches relative to the centres and modes of radiation of the dermal bones, obviously contained the supraorbital and infraorbital divisions of the lateral line system. The canal for the infraorbital lateral line, as it passes through the premaxillae and lachrymal bones, is surrounded by several smaller canals which branch and ramify with the lateral line canal and with each other. These smaller canals must surely have carried vessels and nerves associated with the lateral line organs, including, in all probability, the buccalis lateralis branch of the seventh cranial nerve. The only connections between the canal for the infraorbital lateral line and the medial surface of the dermal bones occur once in the lachrymal bone and once in the premaxilla.

THE NERVES OF THE ETHMOID REGION [1]

The fifth cranial nerve. The ramus profundus of the fifth
cranial nerve leaves the cranial cavity through the space between
the two divisions of the endocranium (see Romer, 1937). Of the
further anterior course of the nerve nothing may be seen until
it re-enters the endocranium through the postnasal wall (Fig. 3,
c.pr.V). Within the nasal cavity the nerve probably divided
into two main branches, a ramus medialis narium and a ramus
lateralis narium (Fig. 6, *r.m.n., r. ln.*), as is the case in the
Dipnoi and Amphibia. However, while the presence of a branch-
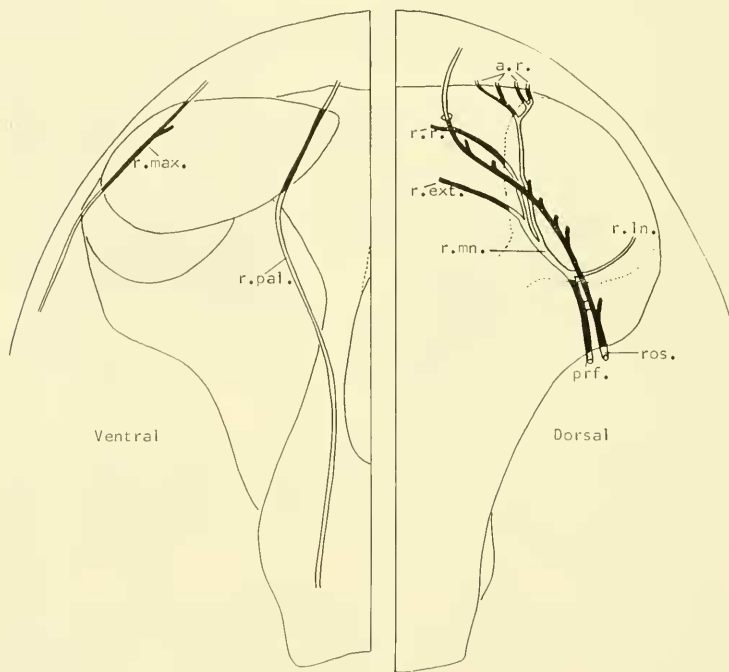ing ramus medialis narium is shown by various canals through

Figure 6. *Ectosteorhachis.* Reconstruction of the nervous system of the
snout. Left in ventral view. Right in dorsal view. Portions of nerve
course represented by an endocranial canal drawn in solid black, recon-
struction in white.

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[1] Unless otherwise stated, the terminology used in this section follows the
system used by Jarvik (1942).

the medial wall of the nasal capsule, similar direct evidence of the path of the ramus lateralis narium is lacking.

The canal which opens out of the nasal cavity just anterior to the opening for the olfactory tract (Fig. 3, *c.r.ext.*) probably contained the "ramus exterior" of the profundus V; this nerve passed dorsally and medially to leave the endocranium at the foramen apicale. Anterior to this a second branch of the profundus V leaves the nasal cavity through the canal opening into the anterior palatal recess (Fig. 3, *c.r.r.*). I have termed this branch the "ramus rostralis" of the ramus medialis narium (Fig. 6, *r.r.*). The canal carrying this nerve has a slight connection with that carrying the ophthalmicus superficialis VII nerve, but anastomosis between these two nerves in this position seems unlikely and the connecting canal probably contained a small vessel. A third set of branches of the ramus medialis narium, which I have termed the "anterior rami" (Fig. 6, *a.r.*), pass through the anterior nasal wall.
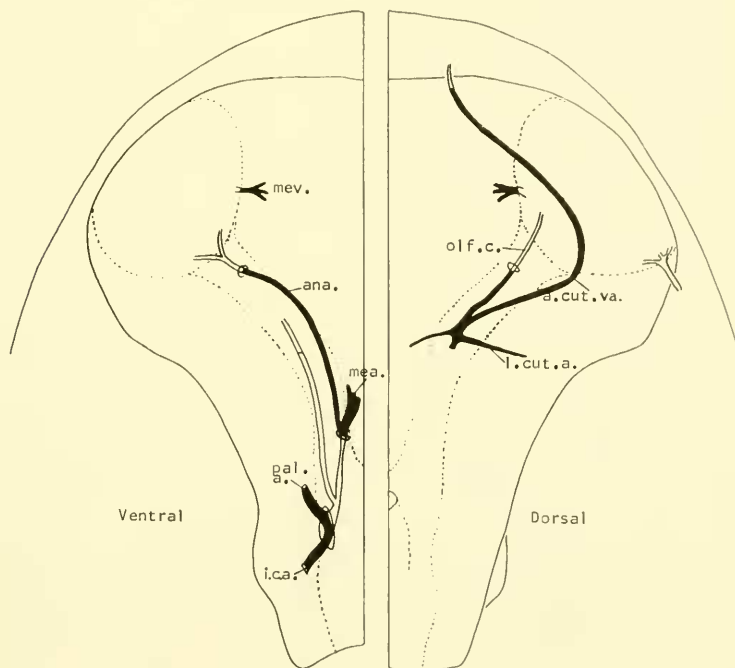

Figure 7. *Ectosteorhachis.* Reconstruction of vascular system. Left in ventral view, right in dorsal view. Portions of vascular system represented by endocranial canals drawn in solid black, reconstruction in white.

The ramus maxillaris of the fifth cranial nerve seems most likely to have been contained in the canal passing through the lateral edge of the vomer (Figs. 4, 8, *l.c.v.*). This nerve (Fig. 6, *r. max.*) thus corresponds to the "r.vot." of Jarvik (1942, fig. 61) and the branch of the maxillary fifth which in *Eusthenopteron* may have formed a post-choanal anastomosis with the ramus palatinus VII. Whether such an anastomosis existed in *Ectosteorhachis* can only be a matter for conjecture.

Other branches of the ramus maxillaris must have passed to and probably within the dermal bones of the anterior part of the cheek. If there was a ramus infraorbitalis it must have entered the nasal cavity at the problematical posteroventral fenestra or have passed forward entirely outside of the nasal cavity.

The seventh cranial nerve. The ramus ophthalmicus superficialis of the seventh nerve enters the endocranium through the canal, in the dorsal part of the postnasal wall, described above (Fig. 3, *c.ros.*VII). As it passes through the endocranium in a curved path corresponding to, but slightly medial to, the path of the supraorbital lateral line canal, the ramus ophthalmicus superficialis gives off a series of fine dorsal branches supplying the lateral line organs. Anteriorly, after emerging onto the surface of the endocranium, the nerve passes forwards and then laterally, curving around to the ethmoid commissure of the lateral line system; however, in this region of the snout it is extremely difficult to trace the finer details of the various nerve pathways.

The ramus palatinus VII seems to have been carried in a canal in the medial part of the vomer (Figs. 4, 8, *m.c.v.*). Anterior to the vomer the nerve probably passed into the anterior palatal recess region; posterior to the vomer it probably passed between the palato-quadrate and parasphenoid bones (Fig. 6, *r.pal.*).

Since the infraorbital lateral line is well developed in *Ectosteorhachis*, the ramus buccalis lateralis VII must also have been present. The path of the infraorbital lateral line in the nasal region (see Thomson, 1964) curves ventrally below the circumnarial bones, and thus in this region the lateral line canal is morphologically ventral to the level of the solum nasi. This being the case, it is unlikely that the ramus buccalis lateralis would have passed within the nasal cavity as it does in the genus *Eusthenopteron* (Jarvik, 1942); furthermore, only in two places, one within the lachrymal bone and one at the very tip of the premaxilla, is there any connection between the canal for the

infraorbital lateral line and the medial face of the bones containing it. (Conceivably the anterior of these two connections served to pass branches of the ophthalmicus superficialis VII to the infraorbital part of the ethmoid commissure.) We have noted above that the canal for the lateral line is, in this region, surrounded by a set of smaller anastomosing canals also contained in the body of the dermal bones, and we must conclude that the ramus buccalis was most likely to have been carried in one of these canals.

THE VASCULAR SYSTEM OF THE ETHMOID REGION

Arterial system. Romer (1937) has already described the arrangement of the internal carotid, palatine, and ophthalmic arteries in the hypophysial region of *Ectosteorhachis;* the further anterior courses of the palatine and ophthalmic arteries cannot be traced in the fossils.

After it has entered the cranial cavity the internal carotid can only be traced by the paths of those of its branches which subsequently leave the cranial cavity. The canals for such branches have been described above. A prominent set of branches (Fig. 4, *cc. mea., c.ana.*) appears to have passed out from the ventral surface of the canal for the olfactory tract just anterior to the separation of the two tracts. A set of three or four median ethmoid arteries (Fig. 7, *mea.*) ramify through the median part of the ethmoid endocranium. They pass right up to the tip of the endocranium, but their most anterior passage is very difficult to follow, since the endocranial bone in this region is extremely cancellous; accordingly I have restored them (Fig. 7) only in a diagrammatic fashion. A single and rather larger canal branching from the endocranial cavity at the same point (Fig. 4, *c.ana.*) also seems to have contained an artery, which I have termed the anterior nasal artery. This artery passes forwards beneath the olfactory tract right up to the nasal region where its canal rejoins that for the olfactory tract and presumably the artery enters the nasal cavity thereby.

The set of canals which branch off from the canal for the olfactory tract dorsally, just posterior to the nasal region, seem most likely to have contained arterial vessels also. I have termed these the cutaneous arteries; there are three main elements, anterior, median and lateral. The anterior cutaneous artery passes forwards dorsal to the olfactory tract and curves over

the nasal region, following approximately the path of the supra-
orbital lateral line canal (Fig. 7, *a.cut.va.*). Immediately after
the separation of this artery from the canal for the olfactory
tract there is a short connection back to this canal (Fig. 7, *olf.c.*)
which may have held a vessel. The series of short connecting
canals between the canals for the anterior cutaneous artery, the
ramus ophthalmicus superficialis VII and the profundus V may
also have carried branches of this anterior artery. The median
cutaneous artery passes anteromedially towards its fellow of the
opposite side (in my material the canals did not appear to meet
as Romer, 1937, had described), and terminates under the pos-
terior part of the median postrostral bone. The lateral cutaneous
artery terminates in the lateral endocranium posterior to the
nasal capsule.

Venous system. There are fewer canals for the passage of
veins in the ethmoid region than for arteries.

A set of branching canals opening into the anterior part of
the posterior median recess of the nasal cavity (Fig. 4, *c.mev.*)
seems to have contained a set of venous vessels draining the
internasal part of the ethmoid endocranium. The finer branches
of these ''median ethmoid veins'' which are not shown in the
restoration (Fig. 7) seem to terminate in the same general region
as do those of the median ethmoid arteries.

The wall of the posterolateral corner of the nasal capsule is
pierced by a canal which may also have contained a small vein,
the lateral nasal vein. This does not enter the nasal cavity (Fig.
3, *c.lat.*), but passes from the space between the dermal bones
of the skull roof to the orbital cavity.

Since the arterial supply to the nasal cavity seems to have
been well developed, there must have been a substantial venous
system draining the nasal chamber. This is borne out by the fact
that the veins draining the internasal wall also pass into the
nasal chamber. There are two alternative routes by which veins
may have left the nasal cavity : either they passed alongside the
profundus nerve in its canal through the postnasal wall, or they
passed through the posteroventral fenestra. There is no way of
deciding between these alternatives. It may, however, be noted
that the posterior opening of the canal for the presumed lateral
nasal vein is in the same general region as the posteroventral
fenestra, and in the absence of some other acceptable explanation
of the function of the posteroventral fenestra, the possibility that
it served for the passage of vascular elements should not be
ignored.

As a final note on the vascular system it should be noted that the canals piercing the anterior wall of the nasal capsule may have contained vessels as well as nerves.

DISCUSSION

The Ethmoid Endocranium

The ethmoid endocranium has been described in the following rhipidistian genera: *Ectosteorhachis* (Romer, 1937, 1941); *Eusthenopteron* (Bryant, 1919; Stensiö, 1922; Holmgren and Stensiö, 1936; Sternberg, 1941; Jarvik, 1937, 1942, 1954); *Glyptolepis* (Jarvik, 1962); *Panderichthys* (Vorobjeva, 1960a); *Platycephalichthys* (Vorobjeva, 1959); *Porolepis* (Jarvik, 1942; Kulczycki, 1960); *Rhizodopsis* (Watson and Day, 1916; Säve-Söderbergh, 1936).

More brief accounts of these and other genera are also to be found in the literature.

Romer (1937) compared the endocranium of *Ectosteorhachis* with that of those forms then known. To this comparison further points may be added, as below.

Anterior palatal recesses.[1] In both *Ectosteorhachis* and *Megalichthys* the anterior palatal recess is divided into two parts by posterior expansions of the premaxillae in the midline. In *Megalichthys* (Thomson, 1964), division is aided by a "buttress" from the anterior part of the endocranium which fits up against the expansions of the premaxillae. In *Panderichthys* (also an osteolepid, see Thomson, 1962), the buttress of the endocranium is present but not the premaxillary expansion (see Vorobjeva, 1960a, fig. 1). In the rhizodontid *Eusthenopteron* the anterior palatal recess is undivided. In *Porolepis* (Porolepidae) and *Holoptychius* (Holoptychidae) the anterior palatal recesses are paired and entirely separate from each other. Each recess consists of a cavum prenasale which corresponds to the anterior recess in Osteolepidae and Rhizodontidae, and a cavum internasale which extends as a shallow depression under the ventral surface of the endocranium (Jarvik, 1942). The two cava internasalia are separated by the anterior part of the parasphenoid; the cava prenasalia are separated by a ridge of the endocranium which may correspond to the "buttress" found in some Osteolepidae.

[1] Also described by the terms "apical pits," "anterior palatal fenestrae."

Jarvik (1942) considered that these anterior palatal recesses in Rhipidistia contained glandular structures homologous with the various intermaxillary glands found in Recent Amphibia. It had already been suggested, however, that these recesses served for the reception of large "tusks" of the lower jaws when the jaws were occluded (Holmgren and Stensiö, 1936; Romer, 1937). Recent work by Kulczycki (1960), Thomson (1962), and Jarvik (1962) has confirmed this view. The characteristic shape of the recesses in the Porolepidae and Holoptychidae reflects merely the nature of the teeth at the tips of the lower jaws which, in these families (Ørvig, 1957; Jarvik, 1962), take the form of a pair of tooth whorls.

Pars ethmoidalis cranialis. Jarvik (1942) stated that in *Porolepis* and typically only in the Porolepidae and Holoptychidae, the cranial cavity in the ethmoid endocranium is continued anteriorly, beyond the point of separation of the canals for the two olfactory tracts, as a large space — the "pars ethmoidalis cranialis." This feature, he stated, was not present in the Osteolepidae or Rhizodontidae.

The inference in Jarvik's work (cf. Jarvik, 1942, fig. 45 A) is that the pars ethmoidalis cranialis contained the hemispheres of the forebrain which were situated anterior to the point of origin of the olfactory tracts. Jarvik thus supposed that the brain of *Porolepis* corresponded in its morphology to that of an urodele such as *Salamandra* (cf. Francis, 1934, pl. 9, figs. 51, 52), as opposed to that of other tetrapods and of *Eusthenopteron* which lack the pars ethmoidalis cranialis and in which the olfactory tracts are given off from the very anterior tip of the forebrain.

A review of the evidence, however, shows that the pars ethmoidalis cranialis does not occur in any consistent manner in the Rhipidistia. Kulczycki (1960) reported that it was absent in the material of *Porolepis* he studied[1] and Vorobjeva (1960a) stated that this cavity was present both in the osteolepid genus *Panderichthys* and the rhizodontid genus *Platycephalichthys* (see Thomson, 1962). When one further bears in mind that the cavity in the endocranium does not necessarily reflect the exact configuration of the brain contained therein, we must conclude that it is far from certain that a structure as inconsistent as the pars ethmoidalis cranialis contained any part of the cerebral anatomy.

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[1] Some of Kulczycki's conclusions must be treated with reservation, since his material consisted only of natural casts.

The nasal capsules and nasal cavity. The nasal capsule has been described in detail only in *Eusthenopteron* and *Porolepis* (Jarvik, 1942; cf. Kulczycki, 1960). Jarvik concluded from his studies that the nasal cavity in *Porolepis* was fundamentally different from that of *Eusthenopteron;* in the following discussion I have compared *Ectosteorhachis* with both of these genera to determine whether or not this distinction may be maintained in the light of a wider comparison.

The nasal capsule and nasal cavity in *Eusthenopteron* (Jarvik, 1942, pp. 464-467) have a complicated configuration. The medial wall of the capsule, as in *Ectosteorhachis,* bears two prominent recesses, an anterior one — termed by Jarvik the ventromedial recess — which is homologous with the anteromedial recess in *Ectosteorhachis,* and a posterior recess into which, as in *Ectosteorhachis,* the olfactory tract enters.

The prenasal wall bears two horizontal ridges which were considered by Jarvik (1942, p. 443) to divide the anterior part of the nasal chamber into various recesses. A lateral horizontal ridge runs from the middle of the prenasal wall onto the lateral nasal wall; a smaller and more medial "erista intermedia" runs to the anterior corner of the medial wall of the cavity. Neither of these ridges is represented in *Ectosteorhachis.*

The lateral wall of the nasal capsule of *Eusthenopteron* bears a thick ledge anterior and ventral to the external narial aperture and projecting as a flange into the nasal cavity. This large structure is termed by Jarvik the "processus intermedius"; its anterior part connects with the lateral horizontal ridge of the prenasal wall. A process from the lateral rostral dermal bone projects onto the processus intermedius and into the nasal cavity as a slip of bone — the processus dermintermedius. These two processes do not have any direct equivalents in *Ectosteorhachis;* the possible homology of the processus intermedius with the crista lateralis of *Ectosteorhachis* is discussed below.

In *Porolepis* (Jarvik, 1942, pp. 367-372, esp. figs. 40, 42; Kulczycki 1960, pp. 74-75, 86-88, fig. 3) there are three main ridges on the inner surface of the nasal capsule, all on the lateral wall. Again, whether these ridges actually reflect any functional division of the nasal sac is uncertain. The most prominent ridge runs from the anterior external naris to the communal opening for the posterior external naris and the choana. It separates the narial openings from the choanal opening, and, being a quite high ridge, has been supposed by Jarvik (1942, p. 402) to have

divided the lateral part of the nasal sac into two recesses, the
more ventral of which he homologises with Jacobson's organ of
urodeles. Jarvik terms this ridge, in accordance with the sup-
posed relation with the Urodela, the crista rostro-caudalis. Kul-
czycki (1960), however, believes that the ventral recess so
delimited is merely a chamber containing the choana and he
terms the ridge "crista subnarina" to avoid hypothetical con-
siderations of phylogeny.

The two other ridges on the lateral nasal wall of *Porolepis* are
the crista orbito-rostralis which runs from the endochoanal notch
to the anteroventral margin of the anterior external naris, and a
thickening of the ventral rim of the fenestra endonarina anterior
which Kulczycki, supposing it to be homologous with the similar
structure in *Eusthenopteron*, terms the process intermedius.

The crista orbito-rostralis is not present as such in either
Ectosteorhachis or *Eusthenopteron*, but it is interesting to reflect
upon the question of the relationship of the crista subnarina
(crista rostro-caudalis) of *Porolepis* to the crista lateralis of
Ectosteorhachis. Both structures are situated anterior to the
(anterior) external naris and pass backwards dorsally to the
choana, separating the choanal recess from the main nasal cham-
ber ; they seem quite likely to be homologous structures.[1]

The crista lateralis is lacking in *Eusthenopteron*, but in this
genus the processus intermedius (and dermintermedius) has
taken over the function of separating the choana and external
naris. We have already noted, above, a possible homologue of
the processus intermedius in the thickening of the ventral mar-
gin of the anterior naris of *Porolepis*, and it is possible to set up
the following scheme by which the various characteristic ar-
rangements of the nasal cavity in *Porolepis*, *Eusthenopteron* and
Ectosteorhachis may be related one to another.

It seems likely that the ancestral form linking the early poro-
lepid fishes to the later Devonian Osteolepidae and Rhizodontidae
was a primitive osteolepid with the external naris situated fairly
far forward; there may even still have been two external nares,
as has been reported for *Panderichthys* (Vorobjeva, 1960a). The
ventral rim of the narial aperture(s) was probably enlarged
as a thick ridge extending backwards to separate the naris from

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[1] If Jarvik is correct in believing that the posteroventral fenestra of
Eusthenopteron (and *Ectosteorhachis*) corresponds to the posterior external
naris, the crista lateralis would have the same relations with the anterior naris,
choana, and posterior naris as the crista subnarina in *Porolepis*.

the choanal recess. This ridge would correspond to the crista subnarina (crista rostro-caudalis) of *Porolepis* and also to a process intermedius. In the Devonian Osteolepidae the more anterior part of the ridge was probably developed into a processus intermedius and this may even have been overlain by a processus dermintermedius from the lateral rostral bone. In the later Osteolepidae the more posterior part of the subnarinal ridge developed as the crista lateralis; this change is probably related to a migration of the narial aperture backwards. There is no dermal process comparable to the processus dermintermedius, and indeed, in *Ectosteorhachis*, the part of the lateral nasal wall bearing the crista lateralis is overlain by the postnarial bone (= tectal of *Osteolepis*, see Thomson, 1964) rather than by that part of the prenarial bone which corresponds to the lateral rostral bone.

The Rhizodontidae seem to have developed from the Osteolepidae. In the rhizodontids the naris has retained its relation to the lateral rostral bone, the processus intermedius is well developed, and the posterior part of the subnarinal ridge is lost. The processus dermintermedius is well developed and may extend onto the prenasal wall of the nasal capsule (Jarvik, 1942). We may conclude that the ethmoid region of the endocranium is apparently constructed according to a single general pattern in *Porolepis*, *Eusthenopteron* and *Ectosteorhachis*. Furthermore, the osteolepid *Ectosteorhachis* is observed to differ from the rhizodontid *Eusthenopteron* no less greatly than either of these genera differs from the porolepid *Porolepis*.

The Nervous System of the Snout

Details of the presumed course of the various nerves of the snout region of Rhipidistia have been given for the following genera only: *Porolepis* (Jarvik, 1942; Kulczycki,[1] 1960); *Eusthenopteron* (Jarvik, 1937, 1942); *Ectosteorhachis* (Romer, 1937). Details of the foramina for the profundus V and ophthalmicus superficialis VII nerves of *Osteolepis* and *Rhizodopsis* are given by Watson (1926) and Säve-Söderbergh (1936), respectively.

The fifth cranial nerve: ramus profundus. In *Ectosteorhachis*, *Megalichthys*, *Osteolepis*, *Rhizodopsis*, and most species and specimens of *Eusthenopteron*, the profundus V enters the nasal

[1] Only the better based of Kulczycki's conclusions are considered here.

capsule by means of a single foramen in the postnasal wall. In *Porolepis*, according to Jarvik (1942), the profundus branches within the orbital region so that two or more rami enter the nasal capsule through separate foramina in the postnasal wall. According to Kulczycki (1960), the profundus in *Porolepis* branched within the postnasal wall itself; this is reported to be the case also in some specimens, at least, of *Eusthenodon* (*Eusthenopteron*) *wenjucovi* (Jarvik, 1937). It must be presumed that in all genera of Rhipidistia the profundus branched either inside or outside the nasal cavity to innervate both the mesial and lateral part of the nasal cavity, but that the actual site of the branching is somewhat variable.

There were most probably two main branches of the profundus within the nasal cavity — the ramus medialis narium and the ramus lateralis narium. In all cases the ramus medialis narium is the better developed, innervating, in addition to the nasal apparatus, the septum nasi and the anteromedial parts of the snout.

In *Eusthenopteron* and *Ectosteorhachis* the only branch of the profundus V to pass out through the dorsal surface of the endocranium is the ramus exterior. In *Porolepis*, according to Jarvik (1942), the profundus V leaves the nasal cavity through several fine canals which pierce the dorsal wall of the nasal capsule. One of the canals he described (1942, fig. 43, c.cut.va.) is homologous with the ramus exterior but, according to Kulczycki (1960), the remainder of these fine canals actually belong to the superficial ophthalmic branch of the seventh cranial nerve and do not arise from the profundus V which is very similar to that of other Rhipidistia.

We have seen that the ramus medialis narium in *Ectosteorhachis* has a number of medial and anterior branches and these are comparable to the branches of this nerve in *Eusthenopteron* (cf. Jarvik, 1942, fig. 61). In Jarvik's restoration (1942, p. 376) the ramus medialis narium of *Porolepis* left the nasal cavity only by means of the dorsal branches mentioned above, but Kulczycki's restoration (1960, fig. 5) includes one anteroventral canal opening into the anterior palatal recess of *Porolepis* which seems to correspond to the naso-basal canal (carrying a terminal branch of the ramus medialis narium through the prenasal wall) in *Eusthenopteron* and *Ectosteorhachis* (Jarvik, 1942, fig. 60, cvn-b; cf. this paper Fig. 3, cc.aa.).

As restored by Jarvik, the ramus lateralis narium in *Porolepis* has branches which leave the nasal capsule through the lateral

nasal wall (Jarvik, 1942, fig. 42A, cc.pr.l.); comparable elements are lacking in *Eusthenopteron* and *Ectosteorhachis*. Jarvik also described in *Porolepis* a third branch of the profundus system which enters the ventrolateral part of the postnasal wall through the "orbitorostral passage" (1942, fig. 42 B, c.cr.). After passing along the ventral surface of the nasal sac this nerve leaves the nasal cavity at a foramen in the prenasal wall, but apparently does not pierce this wall. Kulczycki (1960) found no traces of the orbitorostral passage in his material of *Porolepis*, but he did find a blind canal leading from the nasal cavity into the prenasal wall; this canal, which Kulczycki terms the "paraapical canal," has, however, a different orientation from that
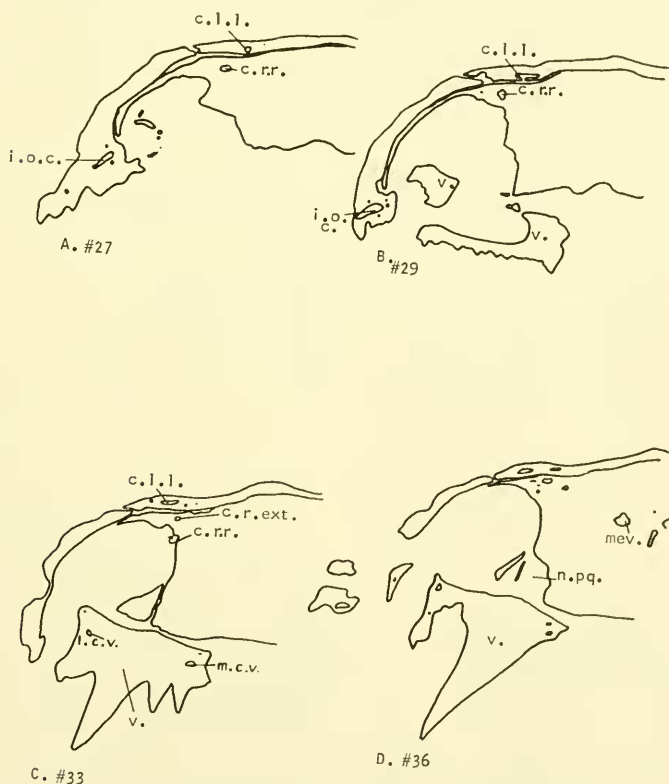

Figure 8. *Ectosteorhachis*. Right nasal cavity, anterior division. #27, at tip of snout; #29 showing anterior margin of vomer; #33 showing anterior margin of external naris; #36 through naris.

described by Jarvik, and in Kulczycki's opinion could only have contained a blood vessel.

We may conclude that the pattern of the ramus profundus V is essentially similar in all Rhipidistia.

Fifth cranial nerve: ramus maxillaris. Jarvik (1942) stated that in *Porolepis* this nerve did not reach as far anteriorly as the nasal region but terminated in the orbit. Kulczycki, however, claimed that there is evidence, in the form of a groove in the lateral nasal wall (Kulczycki, 1960, p. 92), that there was a truncus infraorbitalis extending into the nasal region.

In *Eusthenopteron,* Jarvik (1942, p. 477) traced certain branches of the ramus maxillaris but only part of his restoration is based upon the positive evidence of endocranial canals. What little I have been able to discover of the ramus maxillaris in *Ectosteorhachis* shows that it is generally similar to that of *Eusthenopteron,* but in most major respects our knowledge of this nerve in Rhipidistia is rather unsatisfactory.
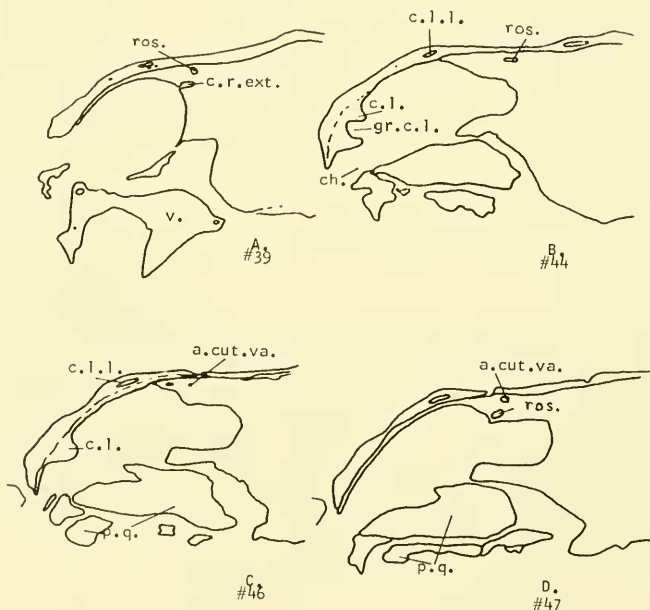

Figure 9. *Ectosteorhachis.* Right nasal cavity, median division. #39 through posterior part of external naris; #44 through crista lateralis; #46 and #47 showing beginning of entry of the olfactory tract canal into the posterior median recess.

The seventh cranial nerve: ramus ophthalmicus superficialis.
In *Eusthenopteron* this ramus passes from the orbit through the
postnasal wall and out onto the dorsal surface of the endocranium
in a canal which has no connection with the lumen of the nasal
cavity. In *Ectosteorhachis* the path of the nerve is exactly the
same, although Romer (1937, fig. 8) mistakenly described the
nerve as entering the nasal cavity. In both genera there may be,
within the postnasal wall, a small canal connecting this nerve
canal with that for the profundus V.

According to Jarvik's (1942) interpretation of the structure of
Porolepis, the ramus ophthalmicus superficialis does not enter
the nasal cavity, but Kulczycki (1960) presents evidence that
the nerve does enter the cavity, either via a separate canal of its
own or through that for the profundus V nerve, and that it passes
along the dorsomedial part of the nasal cavity giving off branches
through the endocranium to the supraorbital lateral line canal.
These branches are the ones that Jarvik (see above) attributed
to the profundus V nerve.

Seventh cranial nerve: ramus buccalis lateralis. Nothing is
known concerning this nerve in *Porolepis*. Jarvik believed that
it might have passed through the orbitorostral passage (the exist-
ence of which has been disputed by Kulczycki). The situation
in *Eusthenopteron* is also vague although Jarvik (1942, pls. 11,
12 and 13) described a gap between the dermal bones and the
nasal capsule in which such a nerve might have passed. *Ecto-
steorhachis* differs from *Eusthenopteron* in that the infraorbital
lateral line canal is situated ventral to the level of the solum
nasi, and the rather meagre evidence available indicates that the
nerve may have been contained in the dermal bones of the
anterior cheek region.

Seventh cranial nerve: ramus palatinus. This nerve seems to
have occupied exactly the same position in *Porolepis*, *Eusthenop-
teron* and *Ectosteorhachis*.

Anastomoses in the nervous system. The two main groups of
living Amphibia, Anura and Urodela, are characterized and may
be distinguished by distinct patterns of anastomoses between
the palatinus VII, maxillaris V and profundus V nerves (e.g.
Coghill, 1902). Jarvik has attempted to show that the Rhipidistia
of the families Porolepidae and Holoptychidae agree in this
respect with the Urodela, and that the families Osteolepidae and
Rhizodontidae agree with the Anura. A main point in Jarvik's
thesis is the position of the anastomosis between the palatinus

VII and the maxillaris V nerves, behind the nasal capsule in the Anura and medial to the choana in the Urodela.

Unfortunately, the evidence concerning possible anastomoses in the Rhipidistia is rather incomplete, although Jarvik (1962) states that he has found new evidence in the anatomy of the poro-lepid *Glyptolepis* to confirm his original suggestions. My material
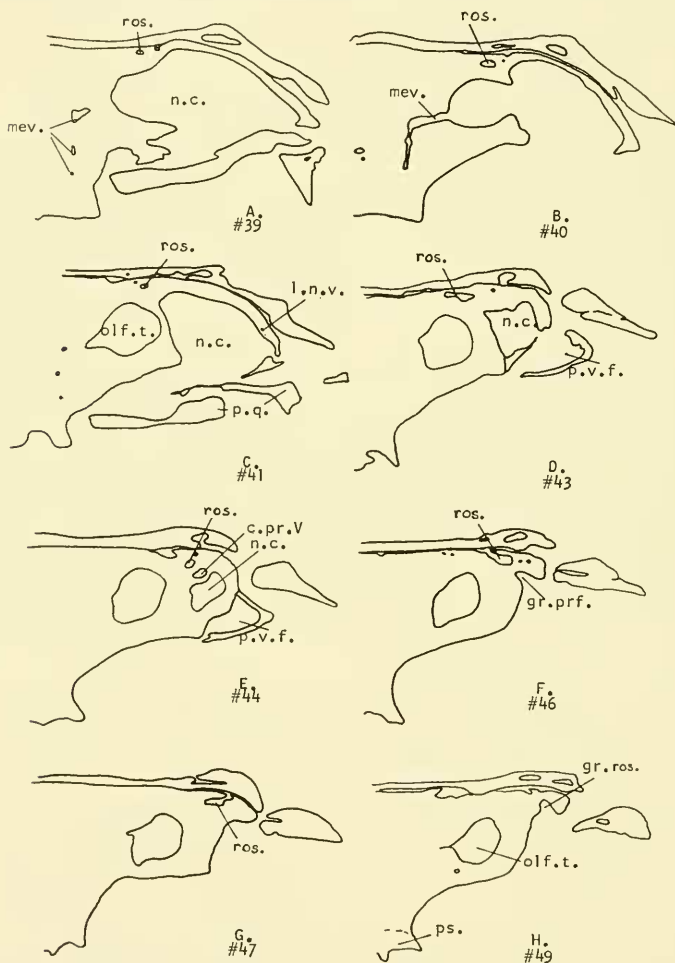

Figure 10. *Ectosteorhachis.* Left nasal cavity. Series of sections through posterior part of the cavity, showing the postnasal wall and the associated nerve canals.

of *Ectosteorhachis* sheds little light on the problem; there is no indication of a connection between the palatinus VII and the maxillaris V as they pass through the vomer or in the space between the vomer and the palato-quadrate.

The canal for the ramus maxillaris V, as it passes through the vomer, gives off one, sometimes two, fine canals to the dorsal surface of the bone, but since the solum nasi is not preserved, I cannot tell whether they might represent evidence of an anastomosis with the branches of the profundus V in the nasal cavity. They may have carried small vessels.

Both the profundus and maxillary rami of the fifth cranial nerve of *Ectosteorhachis* have branches which, as in *Eusthenopteron*, terminate close together in the most dorsal part of the anterior palatal recesses. It is not possible to tell whether or not these nerve branches anastomosed here, although Jarvik states that this was the case.

In summary, we may conclude that in all major respects in which it is fully known, the pattern of the nervous system is essentially similar in *Ectosteorhachis*, *Eusthenopteron* and *Porolepis*.

THE VASCULAR SYSTEM OF THE SNOUT

No thorough review of the vascular system of the snout of Rhipidistia may be made, since the only genus in which it is even moderately well-known is *Ectosteorhachis*. Kulczycki (1960, fig. 5) attempted a reconstruction of the vascular system of *Porolepis*, but this must be treated with reservation. He did, however, find a trace of a canal which might have carried a vena cerebralis anterior — described elsewhere only in *Rhizodopsis*[1] (Säve-Söderbergh, 1936).

What little Jarvik was able to restore of the vascular system of *Eusthenopteron* (1942, p. 480) seems to agree fairly well with the arrangement in *Ectosteorhachis*.

CONCERNING A DIPHYLETIC ORIGIN OF THE TETRAPODS FROM WITHIN THE RHIPIDISTIA

Reference has been made throughout this work to the distinctions that Jarvik (1942) has drawn between the genera *Porolepis* and *Eusthenopteron* with respect to the detailed anatomy

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[1] I have seen the specimen studied by Säve-Söderbergh, but since he used the "shatter technique" it is now impossible to learn anything further from the specimen.

of the snout region. From his study of the snout anatomy of
the Gnathostomata Jarvik drew the following conclusions:

1. That the four families of Rhipidistia may be considered
to belong in two highly distinct groups: the ''Porolepiformes''
(comprising the families Porolepidae and Holoptychidae) and
the ''Osteolepiformes'' (comprising the Osteolepidae and the
Rhizodontidae).

2. That the two major groups of Recent Amphibia, Urodela
and Anura, differ greatly from one another in their snout anat-
omy and must be considered to have arisen separately from
different fish ancestors.

3. That the Urodela differ from the Anura in exactly the
same characteristics as the ''Porolepiformes'' differ from the
''Osteolepiformes,'' and that the Urodela and Anura are direct
descendants of the ''Porolepiformes'' and ''Osteolepiformes''
respectively.

The anatomical study of *Ectostcorhachis* set down above pro-
vides us with a body of new evidence concerning the anatomy
of the ''Osteolepiformes'' which had previously been known
only from study of *Eusthenopteron*. It is now possible to dis-
cuss proposition 1 (above) in considerable (comparative) detail.
Discussions of the interrelationships of the Amphibia belong
elsewhere than in this paper; Parsons and Williams (1962 and
1963), Eaton (1959), Schmalhausen (1959), Szarski (1962) and
others have discussed the evidence for and against a fundamental
separation of the Urodela and Anura. With respect to such
discussion it should be noted that the ancestry of the Recent
Amphibia is known only from very incomplete palaeontological
evidence and discussion relies heavily on evidence from the
anatomy of living forms. I shall confine myself to a considera-
tion of the evidence, in the snout anatomy, for a separation of
the Rhipidistia into ''porolepiforms'' and ''osteolepiforms''
with special regard to the phylogenetic implications of this pro-
posed separation.

In his summary of supposed distinctions between the ''Poro-
lepiformes'' and ''Osteolepiformes'' Jarvik (1942, p. 489, *et
seq.*) enumerated some 26 points by which *Porolepis* (and thus
the ''porolepiforms'') might be interpreted as differing from
Eusthenopteron (and thus, typically, the ''osteolepiforms''). I
propose now to examine each of these points in turn, in the light
of the new evidence presented in the preceding pages.

Several of the 26 points overlap each other and we may group

together first those dealing with the nature of the anterior
palatal recesses and the general arrangement of the ethmoid
endocranium.

1. "The internasal wall in *Eusthenopteron* is narrow and
forms a solid nasal septum. The internasal wall in *Porolepis* is
broad and lodges both the ethmoidal part of the cranial cavity
and the paired cavum internasale" (1942, p. 489).[1]

2. "The divisio prenasalis communis is longer and narrower
in *Eusthenopteron* than in *Porolepis*. On the lateral parts of
its lower face in *Eusthenopteron* are a pair of shallow, ventrally
open prenasal pits, situated far apart from each other; to these
there is no equivalent in *Porolepis*. In *Porolepis*, on the other
hand, the divisio prenasalis communis lodges the paired and
comparatively deep cava prenasalia, which form the direct an-
terior continuation of the cava internasalia and are situated
close to each other" (1942, p. 489).

3. "Point three" states that the "shallow paired" anterior
palatal recesses in *Eusthenopteron* contained intermaxillary
glands directly equivalent to those found in the anterior part of
the palate in the Anura (p. 489, cf. p. 506) and that the cava
internasalia of *Porolepis* contained intermaxillary glands ar-
ranged in the same manner as in Urodela (p. 489, cf. p. 400).

4. "The nasal cavities are fairly close to one another in
Eusthenopteron, whereas they lie far apart in *Porolepis*" (p.
489).

26. "The anterior palatal fenestra in *Eusthenopteron* is
comparatively small, lies entirely in front of the vomers under-
neath the divisio prenasalis communis, and does not form the
ventral opening of any large cavity. The anterior palatal
fenestra in *Porolepis* is large, lies chiefly between the vomers
underneath the internasal wall, and in it are seen the ventral
openings of the cava internasalia and prenasalia" (p. 493).

It should be noted that Jarvik distinguishes in his terminol-
ogy between the apical pits and their "openings" the anterior
palatal fenestrae; I prefer to use the term "anterior palatal re-
cess" for the whole structure. Jarvik states that there are a pair
of "prenasal" (equals "apical") pits in *Eusthenopteron;* but
these are merely the two halves of an essentially undivided
anterior palatal recess (cf. Jarvik, 1942, fig. 56). In *Ectosteo-
rhachis* the anterior palatal recesses are definitely paired, and

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[1] In this and the following quotations, abbreviations and references to figures
in the original text have been omitted.

this is the case in *Megalichthys* and *Panderichthys*, as well as in
Porolepis and *Holoptychius*. It has been noted above that the
cava internasalia of ''porolepiforms'' and the anterior palatal
recesses of ''osteolepiforms'' are homologous structures and that
their characteristic nature reflects only the nature of the teeth
at the tips of the lower jaw rami. Thus there is a difference in the
shape of the recesses in the two groups, but, since no glandular
structures are involved, comparisons with the Recent Amphibia
are not justified.

It has been noted also that the presence or absence of an
ethmoid division of the cranial cavity — the pars ethmoidalis
cranialis — is of random occurrence in the families of Rhipidistia
and does not characterise any particular group.

As has been pointed out in a previous paper (Thomson, 1962),
the internasal wall in the ''osteolepiforms'' may be broad or
narrow and there is no evidence to support the theory that the
presence or absence of the cava internasalia or the pars eth-
moidalis cranialis is correlated simply with the relative width of
the internasal wall or the relative size of the nasal sacs (cf.
Schmalhausen, 1959; Romer, 1962; Szarski, 1962).

5. ''The lamina nariochoanalis is in *Eusthenopteron* formed
by the lateral nasal wall, in *Porolepis* both by the lateral nasal
wall and an adjacent part of the solum nasi'' (1942, p. 490).

The solum nasi is not preserved in *Ectosteorhachis*. But
whereas in the postchoanal region the lateral nasal wall curves
slightly underneath the nasal cavity (Fig. 9, A, B), in the
choanal region this slight ledge is not present (Fig. 8, A, B), and
this may indicate that the lamina nariochoanalis was formed
only by the lateral nasal wall.

6. ''*Eusthenopteron* has no equivalent to Seydel's palatal
process in *Porolepis*'' (p. 490).

Jarvik's identification of a small backwardly directed process
on the anterolateral margin of the choanal aperture in the solum
nasi of *Porolepis* as an homologue of the Seydel's palatal process
of Urodela has been criticized by Kulczycki (1960) who has
pointed out that if the subnarinal crest of *Porolepis* (see above)
is homologised with the crista rostrolateralis of Urodela, then
the small choanal process which lies ''along its prolongation'' is
in a different position from that of Seydel's palatal process in
urodeles. The process was not seen in *Ectosteorhachis*.

7. ''The fenestra endonarina anterior and the fenestra endo-
choanalis are comparatively large in *Eusthenopteron*'' (p. 490).

This does not seem a character of great phylogenetic importance. In *Ectosteorhachis* the fenestra endonarina is relatively slightly smaller than that of *Eusthenopteron*; the fenestra endochoanalis is of the same relative size.

8. "The fenestra endonarina posterior in *Eusthenopteron* is an opening in the postnasal wall leading backwards to the anterior ventro-lateral part of the orbit, and is separated ventrally by an endoskeletal bridge from the fenestra endochoanalis; in *Porolepis* it lies in the lateral nasal wall and is continuous ventrally with the fenestra endochoanalis" (p. 490).

The posteroventral fenestra of *Ectosteorhachis* corresponds to the opening in the postnasal wall of *Eusthenopteron* which Jarvik has homologised with the posterior external naris of *Porolepis*. It is difficult to tell whether Jarvik's proposed homology is justified or not; it seems to me that this fenestra may possibly have been one of the main openings through which the venous vessels left the nasal cavity and it is not impossible that nerve branches passed through it. Jarvik assumed that this fenestra connected by means of a duct (the forerunner of the nasolachrymal duct [1942, p. 537]) with the orbit but since the soft anatomy is not preserved there is no way of checking this hypothesis.

It is interesting to note that Vorobjeva (1960a) has described the osteolepid *Panderichthys* as having two external nares, the posterior of which is confluent with the endochoanal aperture. If this observation is substantiated this genus may thus represent some sort of link between the "Porolepiformes" and the "Osteolepiformes" with respect to this important character.

14. Point 14 refers again to the difference in the relative positions of the posterior external naris in *Porolepis* and its "homologue" in *Eusthenopteron*, and mentions again the possible homology of this structure in *Eusthenopteron* with the tetrapod nasolachrymal duct. This has been dealt with above.

9. "No canal corresponding to the nasobasal canal in *Eusthenopteron* exists in *Porolepis*. On the other hand the orbitorostral passage and the canal *c.vl* in *Porolepis* have no equivalents in *Eusthenopteron*" (p. 490).

The nasobasal canal carried the terminal branch of the ramus medialis narium of the profundus V nerve through the anterior nasal wall into the anterior palatal recess in *Eusthenopteron*; a similar canal is present in *Ectosteorhachis*. As mentioned above, Kulczycki (1960) has noted a canal in *Porolepis* also

which may correspond to this canal.

The orbitorostral passage was not found in *Ectosteorhachis*. Kulczycki could not find this passage in his material of *Porolepis*.

The ''canal *c.vl*'' is something of an enigma; it lies in the lateral part of the postnasal wall of *Porolepis* and was supposed by Jarvik to carry a lateral branch of the profundus V nerve. However, it could very possibly have contained a blood vessel, particularly a vein, draining the nasal cavity. It is not present in *Ectosteorhachis*.

10. ''In *Eusthenopteron* there is a single nerve-canal leading upwards from the nasal cavity to the dorsal face of the ethmoidal region; in *Porolepis* a great many nerve-canals ascend from the nasal cavity to the dorsal face of the ethmoidal region, piercing the dorsal part of the medial nasal wall, the adjacent part of the prenasal wall, and the medial parts of the tectum nasi'' (p. 490).

Point 19 refers to the same subject: ''The n. profundus in *Eusthenopteron* was comparatively weakly developed. . . . The n. profundus in *Porolepis* was strongly developed. . . . In the nasal cavity the medial nasal branch divided into numerous dorsal branches'' (p. 491-492).

As has been noted in the previous discussion, the ramus profundus of the fifth cranial nerve seems to be developed in approximately the same manner in *Porolepis, Eusthenopteron* and *Ectosteorhachis*. The canals passing through the dorsal wall of the nasal capsule of *Porolepis* seem to pertain to the ophthalmicus superficialis VII nerve rather than to the profundus V. Thus, whereas the rami profundi of ''Porolepiformes'' and ''Osteolepiformes'' are similar, there may be a difference in the path of the ophthalmicus superficialis nerve — within the nasal cavity in *Porolepis*, and external to the nasal cavity in *Eusthenopteron* and *Ectosteorhachis*.

11. ''The postnasal wall is pierced in *Eusthenopteron* by a single and not particularly wide profundus canal; in *Porolepis* by a wide medial and one or several narrower lateral profundus canals'' (p. 490).

We have noted above that there may be some variation in the number of canals through which the profundus nerve enters the nasal cavity.

12, 13, 15. Points twelve and thirteen deal with the apparent subdivision of the chamber of the nasal capsule into recesses by

the presence of various ridges and crests on the medial surfaces
of the walls. Point 15 may also be discussed here, since it states
that ''The large differences in the nasal cavity show that there
must have been considerable differences [between *Eusthenopteron*
and *Porolepis*] in the development of the nasal sac'' (pp. 490-
491).

The subject of the ridges and crests of the nasal capsule has
been reviewed above and we have seen that the conditions in
Porolepis, *Eusthenopteron* and *Ectosteorhachis* may possibly be
related to each other. The processus intermedius (or its homo-
logue) may be present in *Porolepis* as well as in *Eusthenopteron*
and the subnarinal ridge seems to be present, slightly modified,
in all three genera.

It is not possible to decide with any degree of certainty
whether or not the apparent morphological subdivisions of the
nasal capsule represent any functional anatomical features of
the nasal sac. For example, the ventromedial recess of *Eusthe-
nopteron* corresponds exactly to that of *Ectosteorhachis,* but
whether this recess of the nasal cavity contained a diverticulum
of the nasal sac, and whether such a diverticulum, if present,
would have contained Jacobson's organ (cf. Jarvik, 1942, pp.
483, 536) cannot be decided from the fossils alone. And while
answers to such questions may be formulated from comparisons
with the Recent Amphibia, the objective purpose of the study
would then be defeated.

16. ''The forebrain in *Eusthenopteron* was of approximately
the same breadth as the diencephalon ; . . . The bulbi olfactorii in
Eusthenopteron lay close to one another immediately in front
of the hemispheres, whereas in *Porolepis* they were situated far
apart at the lateral sides of the hemispheres'' (p. 491).

This apparent distinction arises from interpretation of the
pars ethmoidalis cranialis of *Porolepis* as having contained the
''hemispheres of the forebrain.'' In fact, available evidence now
indicates that the pars ethmoidalis cranialis, which is of random
occurrence throughout the Rhipidistia, did not contain any part
of the brain anatomy, and that the brain of *Porolepis* was
probably not greatly different in overall configuration from
that of *Eusthenopteron.*

17. ''The lateral parts of the snout were in *Eusthenopteron*
supplied mainly by the r. maxillaris V, in *Porolepis* mainly by
the n. profundus'' (p. 491).

There is no doubt that in many adult Urodela, such as

Salamandra, which Jarvik took as his example for the group
(Francis, 1934), the maxillaris V terminates in the orbit, as
Jarvik has suggested is the case in *Porolepis*. But in many
aquatic Urodela and in the larva of *Salamandra*, in which the
lateral line system is retained, the lateral line nerve — ramus
buccalis lateralis VII — is bound into a ''truncus infraorbitalis''
with the maxillaris V nerve. This compound trunk passes an-
teriorly right into the snout region, carrying the maxillaris V
further anteriorly than in the terrestrial Urodela. It has often
been supposed that the Rhipidistia resembled, in their anatomy,
the larvae of Amphibia more strongly than they resembled
adult forms. If, therefore, any traces of the ramus buccalis
lateralis VII nerve are to be found in the porolepid Rhipidistia
then the possibility cannot be excluded that the ramus maxillaris
V was also present.

18. ''In *Eusthenopteron* the r. buccalis lateralis passes for-
wards in the pons nariochoanalis laterally to the choana, giving
off branches to the neuromasts of the anterior parts of the infra-
orbital sensory canal. It terminated far anteriorly near the
very tip of the snout. In *Porolepis* it presumably broke up
into several terminal branches while still in the orbit. One of
these terminal branches, which supplied the foremost neuromasts
of the infraorbital sensory canal, went forwards through the
orbitorostral passage medially to the choana'' (p. 491, cf. Jarvik,
1962).

Kulczycki (1960) has queried Jarvik's restoration of the
orbitorostral passage in *Porolepis*. In *Ectosteorhachis* the nerve
may possibly have passed through the dermal bones of the
snout rather than between these bones and the nasal capsule
as is the case in *Eusthenopteron*. Knowledge of the exact ar-
rangement of the ramus buccalis lateralis in Rhipidistia is far
from satisfactory.

20. ''The r. palatinus VII in *Eusthenopteron* pierced the
anterolateral part of the vomer and during this part of its
course it broke up into three branches . . . In *Porolepis* the
r. palatinus VII probably did not divide during its passage
through the vomer . . .'' (p. 492).

The ramus palatinus VII did not branch during its passage
through the vomer in *Ectosteorhachis*. In this genus, as in
Porolepis, the nerve ran through the medial part of the vomer.

21. Point 21 deals with the fact that Jarvik found traces of
fusion between the tip of the palato-quadrate and the socket

for it in the endocranium, in *Eusthenopteron* but not in *Porolepis* (p. 492).

In *Ectosteorhachis*, as noted by Romer (1937, p. 22), the notch for the reception of the palato-quadrate is not lined by periosteal bone, and thus in this respect *Ectosteorhachis* agrees with *Eusthenopteron*.

22. Point 22 states that the pineal opening, between the "frontal" bones (parietal bones) is characteristically present in "*Eusthenopteron* and other Osteolepiformes" but is absent in Porolepiformes.

In the family Osteolepidae the pineal opening is present in *Osteolepis* and other Devonian forms, but absent in *Megalichthys* and *Ectosteorhachis*.

23. "The vomers in *Eusthenopteron* meet anteriorly in a median suture but their long posterior processes diverge and are separated from one another by the parasphenoid. Each vomer is provided with a descending tooth-bearing lamina. The vomers in *Porolepis* lie mainly in front of the parasphenoid. Their posterior parts are close to one another, but further anteriorly they diverge strongly. They have neither a posterior process nor a descending tooth-bearing lamina" (p. 492).

The vomers of *Ectosteorhachis*, *Megalichthys*, *Glyptopomus*, and probably also *Osteolepis* and *Thursius* (all osteolepids) lack the posterior process of *Eusthenopteron* (Thomson, 1964) ; the vomers in each of these genera lie anterior to the parasphenoid. It seems quite possible, although not all genera are yet well enough known, that the posterior process of the vomer is a special characteristic of the Rhizodontidae.

The vomers of *Ectosteorhachis* but not *Megalichthys* have an anterior tooth-bearing lamina comparable to that of *Eusthenopteron*.

Discussion of the vomers is closely tied up with the next subject — the nature of the parasphenoid.

24. "The parasphenoid in *Eusthenopteron* is narrow and goes forward underneath the ethmoidal region practically to the transition between the internasal wall and the divisio prenasalis communis. The parasphenoid in *Porolepis* is broad and hardly extends forwards onto the lower face of the ethmoidal region" (pp. 492-493).

In the family Osteolepidae a transition may be seen from *Osteolepis* through *Megalichthys* to *Ectosteorhachis* in which the

tooth-bearing median ridge of the parasphenoid becomes pro-
gressively shorter[1] (cf. Thomson, 1964). One very likely ex-
planation of the difference between the relative arrangements of
the vomers and parasphenoid in "Porolepiformes" and "Osteo-
lepiformes" is that their disposition on the anterior part of the
palate is determined by the extent of the anterior palatal
recesses which, as noted above, reflect in their turn the nature of
the anterior dentition of the lower jaws.

In the "Porolepiformes" the anterior palatal recesses are
large and extend posteriorly between the vomers and the para-
sphenoid, hence separating the vomers from one another and
from the parasphenoid and limiting the anterior extent of the
latter. With the evolution of the Osteolepidae (which temporally
and structurally precede the Rhizodontidae), the anterior denti-
tion of the lower jaws changed from a pair of symphysial tooth
whorls (cf. Jarvik, 1962) to a set of simple tusks. Attendant
upon the reduction of the anterior palatal recesses to a (paired)
recess wholly anterior to the vomers and the tip of the endo-
cranium, the parasphenoid came to extend to the tip of the
palate and the vomers were free to extend medially to meet
each other and the tip of the parasphenoid. In the Rhizodontidae
the parasphenoid remained long and the vomers further became
extended posteriorly on either side of it. In the later Osteolepidae
the tooth-bearing ridge of the parasphenoid became secondarily
reduced (cf. *Megalichthys* and *Ectosteorhachis* in Thomson,
1964). The vomers in the Osteolepidae do not seem to have
become as strongly developed mesially as in Rhizodontidae; the
vomers of *Megalichthys* and *Ectosteorhachis* retain an approxi-
mately triangular shape — with their "apices" directed mesially.

As noted by Romer (1937), the parasphenoid of *Ectosteo-*
rhachis is in two parts, a narrow, median tooth-bearing lamina
and a broad thin flange of bone spreading anterolaterally from
the tooth-bearing ridge. The whole is fused to the endocranium.
Unfortunately, it has not been possible to determine whether
this condition is present in other "Osteolepiformes."

25. "The fossa apicalis, intervomerine pit and intervomerine
canal present in *Eusthenopteron* are all absent in *Porolepis*"
(p. 493).

The intervomerine pit is the anterior opening of the inter-
vomerine canal which in *Eusthenopteron* opens into the median

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[1] The specimen of *"Thursius?"* figured by Jarvik (1942, fig. 62B) seems to fit
into this series between *Osteolepis* and *Megalichthys*.

part of the anterior palatal recess. In *Ectosteorhachis*, as in *Porolepis*, the vomers do not meet in a median suture and thus no canal passing between them may be seen in the fossils. The significance of the intervomerine canal is unknown; it may have contained a nerve, vessel, or duct of some kind.

There are obvious limitations to the conclusions that can be drawn from a study of the snout apparatus alone; a broader study of the entire anatomy of the Rhipidistia might lead to results very different from those derived from this restricted series of data. Bearing in mind these limitations, however, it is permissible to reach some interim conclusions as to the relationships of the rhipidistian families to each other and to the tetrapods, from the evidence of the snout anatomy.

In the preceding discussion of the evidences for Jarvik's theory of a basic division of the Rhipidistia, the results of comparative studies seem to show that very many of the characteristics used by Jarvik to distinguish the ''Porolepiformes'' from the ''Osteolepiformes'' no longer support such an hypothesis. However, a limited number of the differences which he claimed are either corroborated by the comparative evidence or were not able to be compared in the material available for study. Thus the following features must still be considered as evidence for Jarvik's theory:

1. There seems to be a difference in the composition of the lamina nario-choanalis.

2. There are differences in the courses of certain blood vessels and minor nerve branches. However, the evidence concerning most of these is in rather an unsatisfactory state, especially for *Porolepis*.

3. A more distinct difference in the nervous system is that in *Eusthenopteron* and *Ectosteorhachis* the ramus ophthalmicus superficialis VII was seen to pass through the tectum nasi, whereas in *Porolepis* this nerve enters the nasal cavity.

4. There seems to be a trend towards lack of mobility of the palatal articulation of the palato-quadrate complex. In both the osteolepid *Ectosteorhachis* and the rhizodontid *Eusthenopteron* the notch in the palate for the reception of the pars autopalatina is not lined with periosteal bone, whereas in *Porolepis* it is.

To these few differences in the nasal region may be added certain features which fall outside the scope of the present study. Jarvik (1962) has described differences in the structure

of the branchial arch apparatus of *Eusthenopteron* and *Glyptolepis*. Investigation of the branchial arch apparatus of other rhipidistians has yet to be made. Ørvig (1957) has described the microscopic structure of the scales of the Rhipidistia, and Jarvik (1962) considers that the evidence presented by Ørvig further substantiates his interpretation of rhipidistian relationships. Another feature is the difference in the nature of the anterior dentition of the lower jaws (cf. Jarvik, 1962; Thomson, 1962; and above).

In discussing the significance of the various anatomical features of the Rhipidistia, it must be borne in mind that two separate discussions are involved; on the one hand, there is the problem of the classification of the Rhipidistia themselves, and on the other hand, there is the problem of the relationship of the Rhipidistia to the tetrapods. Jarvik has endeavoured to show that these two problems are but two sides of the same coin. He delineates two basic groups of fishes in terms, principally, of their supposed anatomical relationship to the two "separate" groups of Amphibia. However, the main conclusion of the present study must be that, on the evidence of the snout anatomy, the three families of Rhipidistia investigated (Porolepidae, Osteolepidae and Rhizodontidae) are constructed according to a common anatomical plan. Furthermore, and most importantly, this overall similarity in structure is particularly manifest in the majority of those characters (the pattern of the nervous system, nature of the internasal wall, etc.) which Jarvik considered to be diagnostic of the specific relationships of the "porolepiforms" and urodeles, on the one hand, and the "osteolepiforms" and the anurans, on the other hand. Thus, from the detailed review of the comparative anatomy of the rhipidistian snout, given above, we must come to the conclusion that there is no substantial evidence in these structures to support the supposition that any particular family of Rhipidistia is more closely allied to one particular group of Amphibia than to another. There is no evidence to support the particular diphyletic theory of the origin of the tetrapods proposed by Jarvik.

We may now turn to examine Jarvik's proposition that the Rhipidistia comprise two separate stocks — "porolepiform" and "osteolepiform." We may accept the fact that the families Porolepidae and Holoptychidae are very closely allied. But to balance the apparent distinctions between these fishes and the

combined Rhizodontidae and Osteolepidae, noted in the preceding paragraphs, we may take note of the very numerous resemblances between the four families of Rhipidistia — resemblances which indicate the essential unity of the group as a whole (Schmalhausen, 1959, 1960; Romer, 1962; Thomson, 1962; Szarski, 1962). Most importantly we may note that in certain features, such as the structure of the scales (Ørvig, 1957), the configuration of the nasal apparatus, and possibly also the arrangement of the vomers and parasphenoid on the palate, the Osteolepidae differ from the Rhizodontidae as greatly as they differ from the Porolepidae and Holoptychidae combined. Such considerations led Berg (1958) to consider the Rhipidistia as being made up of *three* main groups — the Porolepiformes, the Osteolepiformes and the Rhizodontiformes. Such a scheme seems more correctly to assess the interrelationships of the four families than does that of Jarvik. Assignation of ordinal rank to each group has the disadvantage of over-emphasizing the differences between the families. A more satisfactory arrangement would be to consider each group as no more than a superfamily.

In summary we may conclude:

1. That the four families of Rhipidistia are, anatomically, a close-knit assemblage.

2. The interrelationships of the Rhipidistia may not be expressed by a simple separation of ''Porolepiformes'' and ''Osteolepiformes,'' but rather the Rhipidistia may be thought to comprise three superfamilies, the Holoptychoidea, Osteolepoidea and the Rhizodontoidea, of equal rank.

3. There is no evidence in the anatomy of the rhipidistian snout to indicate a diphyletic origin of the urodele and anuran Amphibia from within the Rhipidistia.

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ABBREVIATIONS USED IN THE FIGURES

a.cut.va.	anterior cutaneous artery
a.m.r.	anterior median recess
ana.	anterior nasal artery
a.p.r.	anterior palatal recess
a.pr.	anterior postrostral
a.r.	anterior rami (of profundus)
c.ana.	canal for anterior nasal artery
cc.aa.	canals through anterior nasal wall
cc.mea.	canals for median ethmoid arteries
ch.	choana
c.l.	crista lateralis
c.l.cut.va.	canal for lateral cutaneous artery

c.lat.	canal for lateral nasal vein
c.l.l.	lateral line canal
c.max.	canal for maxillary V nerve
c.m.cut.va.	canal for median cutaneous artery
c.mev.	canal for median ethmoid vein
c.o.s.	canal for ramus ophthalmicus superficialis VII
c.pal.	canal for palatine VII nerve
c.pr.V	canal for profundus V nerve
c.r.ext.	canal for ramus exterior (of profundus)
c.ros.VII	canal for ramus ophthalmicus superficialis VII.
c.r.r.	canal for ramus rostralis (of profundus)
ds.	dermosphenotic
e.n.	external naris
f.ap.	foramen apicale
f.cut.va.	foramen for medial cutaneous artery
ff.ros.	foramina for ramus ophthalmicus superficialis VII
gr.c.l.	groove on medial face of crista lateralis
gr.prf.	groove for profundus nerve
gr.ros.	groove for ophthalmicus superficialis VII
g.s.o.l.	groove for supraorbital lateral line
i.c.a.	internal carotid artery
i.o.c.	canal for infraorbital lateral line
i.o.l.	infraorbital lateral line
l.c.v.	lateral canal in vomer
l.cut.a.	lateral cutaneous artery
l.n.v.	lateral nasal vein
m.c.v.	medial canal in vomer
mea.	median ethmoid arteries
mev.	median ethmoid veins
m.pr.	median postrostral
n.	nasal
n.c.	nasal cavity
n.pq.	notch for palato-quadrate
n.prf.	notch for profundus nerve
n.ros.	notch for ramus ophthalmicus superficialis
n.r.p.	naso-rostro-premaxilla
n.t.	tube of external naris
olf.c.	connection of anterior cutaneous artery back to canal for olfactory tract
olf.t.	olfactory tract
pa.	parietal
pal.a.	palatine artery
pin.f.	pineal foramen
pm.t.	premaxillary tusk
p.n.	postnarial
p.q.	palato-quadrate
p.rec.	posterior median recess

prf.	profundus V nerve
pr.n.	prenarial
p.v.f.	parasphenoid
ps.	posteroventral fenestra
r.ext.	ramus exterior (of profundus)
r.ln.	ramus lateralis narium (of profundus)
r.max.	ramus maxillaris V
r.mn.	ramus medialis narium (of profundus)
ros.	ramus ophthalmicus superficialis VII
r.pal.	ramus palatinus VII
r.r.	ramus rostralis (of profundus)
rr.a.	anterior rami (of profundus)
s.o.l.	supraorbital lateral line
v.	vomer